



# Accounting for sex-specific differences in gene flow and functional connectivity for cougars and implications for management

Katherine A. Zeller · Claudia Wultsch · Lindsay S. Welfelt · Richard A. Beausoleil · Erin L. Landguth

Received: 19 May 2022 / Accepted: 7 November 2022 / Published online: 23 November 2022

This is a U.S. Government work and not under copyright protection in the US; foreign copyright protection may apply 2022

## Abstract

**Context** Maintenance of connectivity is a commonly recommended strategy for species management and conservation as habitat loss and fragmentation continues. Therefore, functional connectivity modeling is needed for species over large geographic areas. However, sex-specific functional connectivity is rarely considered, even though the results of such

an analysis have the potential to influence applied management practices.

**Objectives** We use a large ( $n=1902$ ) genetic dataset to identify population level and sex-specific functional connectivity for cougars in Washington, USA.

**Methods** We conducted a landscape genetics analysis that pseudo-optimized resistance surfaces for the full sample of cougars as well as for male and female groups. We then modeled connectivity across the top performing resistance surfaces with resistant kernels.

**Results** The top resistance surface for females had higher resistance and lower connectivity than the males and had more spatial variability. However, we also observed greater resistance to movement and a lack of connectivity for males in and around the Olympic Peninsula. The resistance surface and connectivity models for all cougars contained both the broad features of the male models and the more heterogeneous features of the female models, indicating the importance of both local and regional dispersal and breeding.

**Conclusions** In species with sex-specific differences in movement and dispersal, accounting for these differences can be important for understanding functional connectivity. For cougars in Washington, this revealed depressed connectivity for males on the Olympic Peninsula which may indicate a more immediate management concern for the future of this population than previously thought.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10980-022-01556-z>.

K. A. Zeller (✉)  
Aldo Leopold Wilderness Research Institute, Rocky Mountain Research Station, US Forest Service, Missoula, MT, USA  
e-mail: [katherine.zeller@usda.gov](mailto:katherine.zeller@usda.gov)

C. Wultsch  
Bioinformatics and Computational Genomics Laboratory, Hunter College, City University of New York, New York, NY 10021, USA

C. Wultsch  
Sackler Institute for Comparative Genomics, American Museum of Natural History, New York, NY 10024, USA

L. S. Welfelt · R. A. Beausoleil  
Washington Department of Fish and Wildlife, 3515 State Highway 97A, Wenatchee, WA 98801, USA

E. L. Landguth  
Computational Ecology Lab, School of Public and Community Health Sciences, University of Montana, Missoula, MT 59812, USA

**Keywords** *Puma concolor* · Landscape genetics · Resistant kernels · Connectivity · Resistance · Dispersal

## Introduction

Many wildlife populations are increasingly susceptible to the negative effects of human development. Habitat loss and fragmentation decrease the availability of resources and increase isolation, placing wildlife, especially carnivores, at higher risk of extirpation (Di Minin et al. 2016; Crooks et al. 2017). To combat the negative effects of habitat loss and fragmentation, habitat protection paired with maintaining and restoring broad-scale landscape connectivity are commonly recommended (Heller and Zavaleta 2009). Therefore, identifying both the spatial distribution of habitat and areas of connectivity is important for effective species conservation and management in the Anthropocene.

One of the fastest growing states in the USA is Washington (US Census, [www.census.gov](http://www.census.gov)), and in the Puget Sound area alone, the human population is expected to almost double by the year 2050 (Puget Sound Regional Council, [psrc.org](http://psrc.org)). This may result in increased development which could elevate the risk of isolation for some cougar (*Puma concolor*) populations in the state. Warren et al. (2016) and Wultsch et al. (*in review*), found that cougars in some areas of Washington had relatively low allelic diversity and levels of gene flow. In particular, the Olympic Peninsula may be an area of conservation and management concern as it had the lowest genetic variation, highest inbreeding coefficient, and lowest immigration rates of any other site in the state. Interestingly, Wultsch et al. (*in review*) also found that the Olympics had relatively high emigration rates, but that immigration into the area from other populations was low.

Other cougar populations that are isolated by roads and development, such as those in southern California, have low heterozygosity—with the values for some populations approaching those of the endangered Florida panther (Gustafson et al. 2019). Despite the general ability of cougars to move and disperse long distances (Stoner et al. 2008; Hawley et al. 2016), dispersal to and from these populations is limited due to large freeways and intense human development (e.g., Ernest et al. 2014). Currently, efforts to increase genetic variation and reduce inbreeding

in these populations are limited to multi-million-dollar road crossing structures or translocation of individuals. Heterozygosity of the cougar population on the Olympic Peninsula was not reported to be as low as those in Florida and California, but with the projected human development in this region, identifying and maintaining areas of connectivity could help prevent further isolation and offset the need for costly interventions. These concerns are not isolated to the Olympic Peninsula population: Wultsch et al. (*in review*) found that asymmetrical migration rates and source-sink dynamics were identified for other populations in Washington. Therefore, maintaining connectivity across the entire state has ecological importance.

Connectivity models are often derived from species-specific observational or movement data, but can also be derived from genetic data (Zeller et al. 2012). Movement data excels at capturing fine scaled, real-time movement decisions by individuals. However, genetic data have the added advantage of reflecting not only movement, but also successful dispersal and breeding over generations. Therefore, functional connectivity based on genetic data represents broader scale population processes. To model connectivity with genetic data, a landscape genetics approach can be used that models genetic distances among populations or individuals as a function of resistance distance (McRae 2006) among those same points. Resistance distances are calculated across landscape features and transformed into resistance or cost to movement values. Landscape genetic model results therefore estimate the resistance of natural and anthropogenic landscape features to movement, and can be used as the basis for connectivity models. Warren et al. (2016), conducted such a landscape genetics study to identify resistance to gene flow for cougars across the state. The study found that forest cover was the main driver of gene flow and no other variables, aside from Euclidean distance, were significant in predicting genetic distance. Warren et al. (2016) acknowledged that other factors were likely contributing to cougar gene flow in Washington, but that they were not able to capture these factors in their analysis—nor did they model connectivity.

Since the Warren et al. (2016) study, landscape genetic approaches have advanced and collection of genetic samples by Washington Department of Fish and Wildlife (WDFW) has continued, resulting in

an almost tripling of the number of individual cougars available for analysis. Here, we conducted a landscape genetic analysis for cougars ( $n=1902$ ) in Washington, USA, and southern British Columbia, Canada, to understand what variables are influencing gene flow and to predict a surface that estimates resistance to gene flow movement. Given the sex-specific differences in genetic diversity indices described in Wultsch et al. (*in review*), and known sex-specific differences in cougar dispersal behavior (Sweanor et al. 2000; Stoner et al. 2006; Thompson and Jenks 2010), we analyzed the entire population of samples and then conducted analyses for males and females separately. We predicted that males, given their longer dispersal distances, would drive population-level gene flow (Sweanor et al. 2000). Based on the results of Warren et al. (2016), we predicted that forest cover would enhance gene flow across the study area, but we also predicted that human development variables would impede gene flow. Other landscape genetic studies in Idaho, California, and the southwestern USA have found urban development, agriculture, and roads influenced genetic differentiation and resistance (Balkenhol et al. 2014; Naidu 2015; Zeller et al. 2017). We used the predicted resistance surfaces from our landscape genetic analysis to model connectivity for cougars across the study area and produce spatially explicit maps for management and conservation of cougar movement and gene flow.

## Methods

### Study area

The study area was statewide in Washington, USA and the mid-southern region of British Columbia, Canada (Fig. 1). Climates and vegetative communities vary considerably across the study extent from temperate rainforests in the west, to the sagebrush steppe of the Columbia Plateau, to dry coniferous forests in the east. Genetic data were mostly collected in and around the Olympic Peninsula, the Cascade Range, the Selkirk and Kettle Ranges, and the Blue Mountains.

The Olympic Peninsula (Fig. 1a) is a temperate, maritime rainforest that ranges from sea level to 2400 m in elevation in the Olympic Mountains. Annual precipitation varies in the Olympic Mountains

but averages 152 to 406 cm. Annual average minimum temperature in January is  $-1^{\circ}\text{C}$  and the average maximum temperature in July is  $23^{\circ}\text{C}$ . Common prey species include black-tailed deer (*Odocoileus hemionus columbianus*), elk (*Cervus elaphus*), and beavers (*Castor canadensis*).

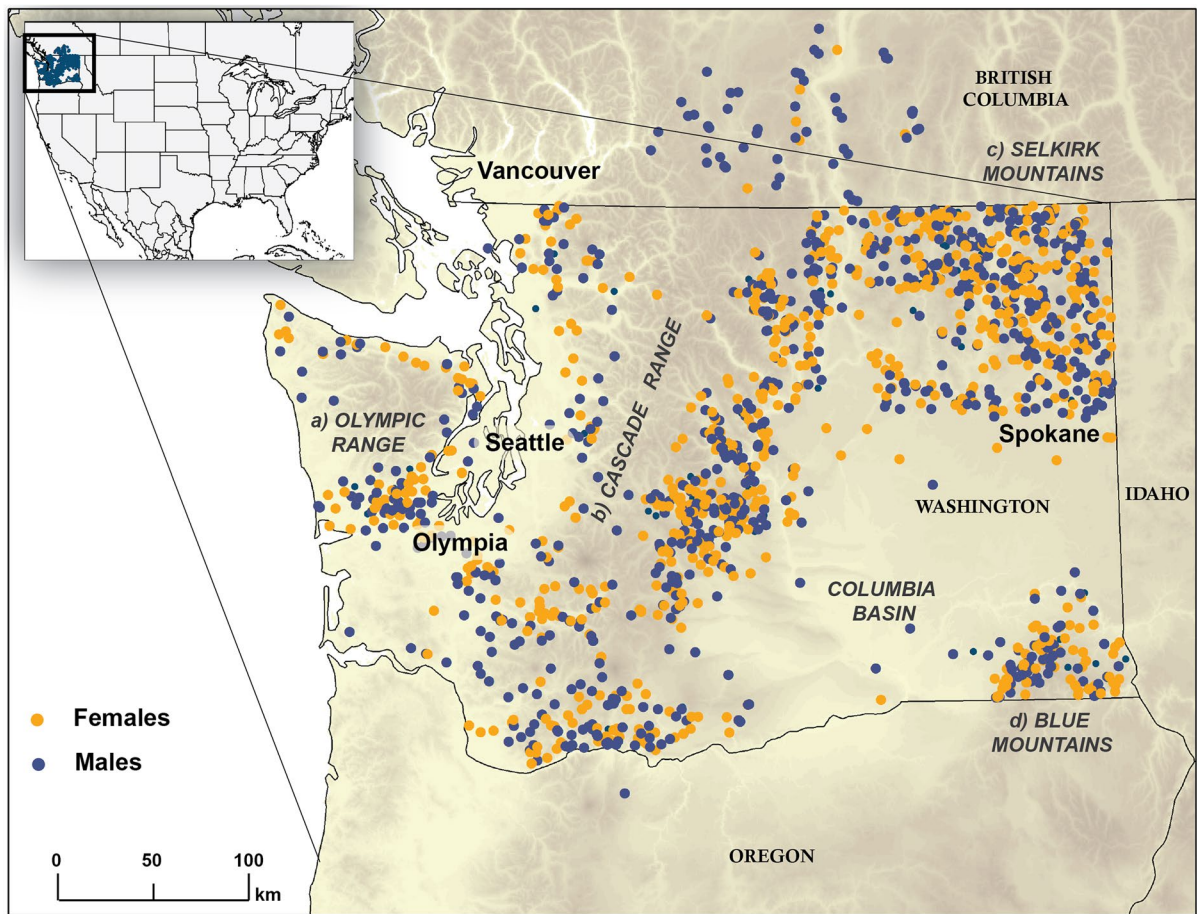
The Cascade Mountains (Fig. 1b) are rugged with elevations ranging from sea level to almost 4400 m at Mount Rainier. The western slopes experience a maritime climate with an annual average precipitation of 251 cm, while precipitation on the eastern slopes varies from 25 to 254 cm annually depending on location. Annual average minimum temperature in January is  $-4^{\circ}\text{C}$  and the average maximum temperature in August is  $21^{\circ}\text{C}$ . Common prey species include black-tailed deer, mule deer (*O. hemionus*), white-tailed deer (*O. virginianus*), and elk.

The Selkirk and Kettle Ranges (Fig. 1c) are characterized by mountainous terrain in the southern portion of the Selkirk Range, with elevations ranging from 500 m to 2200 m. Annual precipitation averages 48 cm. Annual average minimum temperature in January is  $-9^{\circ}\text{C}$  and the average maximum temperature in August is  $25^{\circ}\text{C}$ . Primary prey consists of white-tailed deer, mule deer, elk, and moose (*Alces alces*).

The Blue Mountains (Fig. 1d) in southeast Washington represents the northern portion of this mountain range, which is part of the Columbia Plateau. Elevations range from several hundred meters above sea level along the major drainages of the Snake and Columbia Rivers to 1950 m on Oregon Butte. The region is characterized by hot dry summers and mild winters with mean temperatures ranging from  $-7^{\circ}\text{C}$  in January to  $37^{\circ}\text{C}$  in July. Annual precipitation, averaging 76 cm, falls primarily as snow between November and February. Prey in this area consists of mule deer, white-tailed deer, and elk.

### Genetic sampling

Cougar tissue samples were obtained across Washington by WDFW personnel from 2003 to 2018. Overwhelmingly, tissue samples were obtained during mandatory inspections of hunter kills. A much smaller number of samples were opportunistically included from research captures statewide. Additional samples from south-central British Columbia were obtained in cooperation with compulsory inspectors for the British Columbia Ministry of Forests, Lands



**Fig. 1** Male and female cougar genetic sample locations and greater study area in Washington, USA and south-central British Columbia, Canada, 2003–2018

and Natural Resource Operations from 2003 to 2010. Genetic samples were assigned to the GPS coordinates of the kill or capture, when possible, or inferred using geographical descriptions given by hunters. Capture locations were accurate, however hunter collected information was estimated to be accurate to 10 km. Tissue samples were processed and genotyped at 18 microsatellite loci by WDFW's Molecular Genetic Laboratory (more information provided in Warren et al. 2016 and Wultsch et al. *in review*). Loci were polymorphic with a total of 108 alleles detected and an average of 6 alleles per locus. Mean observed and expected heterozygosity was 0.52 and 0.59, respectively. Genotyping resulted in identification of 1,825 individuals in Washington state (896 females, 853 males, 98 unknown sex), and 55 individuals in British Columbia (6 females, 49 males), for a total of

1,902 cougars. Population genetic analyses of these data are presented in Wultsch et al. (*in review*).

#### Landscape data

We selected 11 variables known to affect cougar habitat use, movement, and gene flow. These included topographic, human development, and vegetation variables (Table 1). All variables were projected to the Albers Conic Equal Area projection and resampled to a 90 m pixel size. Other studies have demonstrated cougars respond to environmental variables at different spatial scales (Wilmers et al. 2013; Zeller et al. 2017). Therefore, to determine the scale of effect (Jackson and Fahrig 2015; McGarigal et al. 2016) for cougar gene flow for each variable in our study, we smoothed the variables with a Gaussian kernel

**Table 1** Geospatial variables used for developing landscape genetic resistance models for cougars in Washington, USA, and south-central British Columbia, Canada, 2003–2018

	Variable	Description	Source
Development	Road density	Line density of primary, secondary, and tertiary roads	Derived from Open Street Map Contributors (2020)
	Building density	Point density of Microsoft building footprint data set calculates as buildings per square kilometer	Microsoft building footprint data (2019)
Land cover	Percent tree cover	Percent tree cover	Hansen et al. (2013)
	Shrubs	Shrubs from U.S. National Land Cover Database and British Columbia Baseline Thematic Mapping Data	British Columbia Government (2019); Yang et al. (2018)
	Grassland	Grasslands from U.S. National Land Cover Database and British Columbia Baseline Thematic Mapping Data	British Columbia Government (2019); Yang et al. (2018)
	Agriculture	Agriculture from U.S. National Land Cover Database and British Columbia Baseline Thematic Mapping Data	British Columbia Government (2019); Yang et al. (2018)
	Rivers and streams	Rivers and streams from the National Hydrography data set and the British Columbia Freshwater atlas	USGS (2017); British Columbia Government (2015)
Topography	Elevation	Digital elevation model	USGS (2016)
	Terrain ruggedness index	Calculated from the digital elevation model using the ‘terrain’ function in R (Hijmans 2021)	
	Ridges	Derived from topographic position index, which was calculated from the digital elevation model using the ‘terrain’ function in R (Hijmans 2021)	
	Canyons	Derived from topographic position index, which was calculated from the digital elevation model using the ‘terrain’ function in R (Hijmans 2021)	

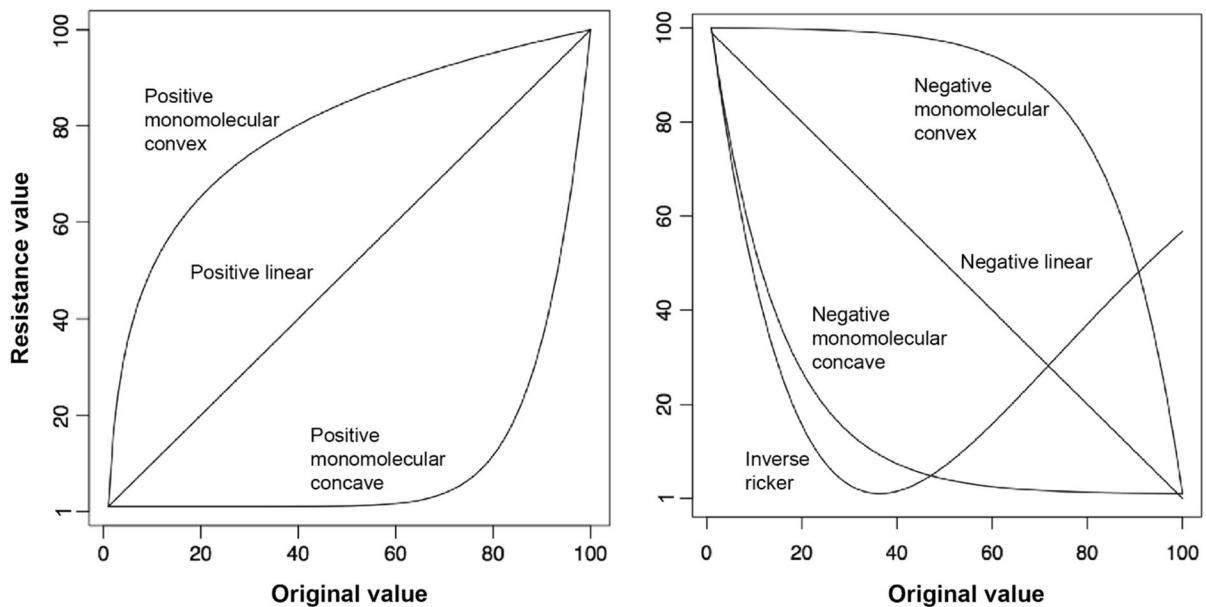
at the following bandwidths, 90 m, 500 m, 1500 m, and 3000 m. These bandwidths correspond to the average movement rate of cougars in Washington State over 10 min, 2 h, 6 h, and 12 h (Kertson et al. 2011) — time periods over which cougars may be making movement decisions and responding to landscape features. Smoothing was performed with the ‘smoothie’ package (Gilleland 2013) in R software (R Core Team 2021).

#### Resistance surface generation

For each geospatial variable, the raw values were converted to resistance (where high resistance equates to low levels of gene flow and vice versa). We did not assume a relationship between the raw values of an environmental layer and resistance to gene flow a

priori. Instead, we tested seven different transformational forms (from Peterman 2018) to determine the most appropriate transformation; three representing positive relationships, three representing negative relationships, and one representing a curvilinear relationship similar to a quadratic (Fig. 2). For the positive linear, positive monomolecular convex, and positive monomolecular concave transformations, resistance increased with increasing values of a variable. For the negative linear, negative monomolecular convex, and negative monomolecular concave transformations, resistance decreased with increase values of a variable. The inverse ricker transformation represented cases where moderate values of a variable had the lowest resistance. We transformed each scaled variable by range rescaling the surface from 1 to 100 and then applied each transformation to create





**Fig. 2** Transformations tested to obtain genetic resistance hypotheses for development, land cover, and topographic variables at various spatial scales for cougars in Washington, USA, and south-central British Columbia, Canada, 2003–2018

resistance surfaces with values from 1 to 100. This process created 336 univariate resistance hypotheses. Due to computational limitations with the landscape genetic models, and uncertainty in spatial location of some hunter harvested samples, we resampled all layers to a 900 m pixel size for analysis.

#### Landscape genetic analysis

We calculated pairwise Euclidean distances among the 1902 individuals and generated a Euclidean distance matrix with the ‘rdist’ package (Blaser 2020) in R. For genetic distance, we calculated the proportion of shared alleles among all pairwise individuals and generated a genetic distance matrix with the ‘adegenet’ R package (Jombart 2008; Jombart and Ahmed 2011). A recent study has demonstrated that the proportion of shared alleles performed well for predicting the relationship between genetic distance and landscape distance with large sample sizes ( $n > 1000$ ) (Shirk et al. 2017). We calculated resistance distance between all pairwise sample locations across each univariate resistance hypothesis with the costDistance function in the ‘gdistance’ package (van Etten 2017) in R. We then fit a univariate linear mixed effects model that accounted for the pairwise

structure of distance matrices with the maximum likelihood population-effects method (MLPE; Clarke et al. 2002; Van Strien et al. 2012), using code from the ‘ResistanceGA’ package (Peterman 2018; Peterman et al. 2014) with restricted maximum likelihood set to false. In these models, the genetic distance matrix was our response variable, and the resistance distance matrix and Euclidean distance matrices were our predictor variables. The MLPE method has been shown to outperform other popular correlation methods in landscape genetics such as multiple regression with distance matrices or causal modeling with Mantel tests (Shirk et al. 2018). Furthermore, Row et al. (2017) found performance of MLPE models to increase with the addition of Euclidean distance as a variable. This helps to further account for the auto-correlation structure of pairwise distance matrices and reduces the selection of spurious variables (Row et al. 2017). We also ran a model to test the isolation by distance hypothesis by only using the Euclidean distance matrix as the predictor variable.

We evaluated the univariate resistance hypotheses for a variable by comparing Akaike’s Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002) values. The model with the lowest AICc value for a variable was

identified along with the scale and transformation to resistance. We also calculated BIC and marginal  $R^2$  for the models with the ‘MuMIn’ R package (Nakagawa and Schielzeth 2013; Bartoń 2019) to assess variance explained by a predictor. Conditional  $R^2$  values are also reported. We based model selection on the AICc values since Row et al. (2017) found marginal  $R^2$  values were biased toward more complex models.

For our multi-variable hypotheses, instead of including each variable in the model in the traditional additive fashion, we summed all variables in a model to create a single resistance surface across which resistance distance was calculated. This approach correctly collapses all sources of resistance into a single layer and estimates the genetic distance response across this composite surface (Peterman and Pope 2021). Peterman and Pope (2021) pointed out that individuals moving across a landscape are not parsing out the individual contributions of each landscape element (e.g., land cover type vs elevation vs development), but are instead responding to the aggregate landscape. Therefore, our multi-variable procedure was as follows: (1) we summed all combinations of the final variables at their selected scale and resistance transformation; (2) we rescaled the summed surfaces from 1 to 100; (3) we calculated resistance distance across these composite surfaces; and (4) we fit MLPE for each composite surface including Euclidean distance as an additional variable as above. We assessed cost distance correlations among predictor variables with partial mantel correlations using the vegan package (Oksanen et al. 2022) in R and only ran models with variables below a correlation of 0.61 (Correlation matrices are provided in Appendix 2). We again compared models with AICc values and report the composite resistance model with the lowest AICc value.

We repeated the above procedure for females and males separately to determine if there were any sex specific effects of landscape structure on cougar gene flow. To help interpret our findings, we also calculated the local extent of breeding, or sigma, for males and females (Shirk and Cushman 2014). Specifically, we used the ‘sGD’ R package (Shirk and Cushman 2011) to infer the radius of Wright’s genetic neighborhood (Wright 1946) from the male and female cougar genotypes.

## Functional connectivity analysis

We assessed connectivity with resistant kernels (Compton et al. 2007) which accumulate cost and distance from source points placed on the landscape and result in a continuous surface that represents movement density across the landscape. We sampled 20,000 points across the study area with the ‘Create Spatially Balanced Points’ tool (Theobald et al. 2007) in ArcMap 10.5.1 (ESRI 2016) as follows. We took the linear inverse of the top resistance surface and rescaled it from 0–1. We also masked out areas of high building density, so we only sampled source points in areas that had a building density of <25 buildings/km<sup>2</sup>. We used this tool to sample points more frequently in areas of low resistance while still obtaining a good coverage of source points across the study area. We then used these source points along with the top resistance surfaces to create resistant kernels with the software UNICOR (Landguth et al. 2012). Resistant kernels require a cost distance threshold to be specified where the kernels will stop spreading from each source point when the threshold is reached. We used 500,000 as the cost distance threshold for cougars in Washington, which would be equivalent to a distance of 500 km across a landscape with no resistance. We selected this value since it is double the maximum dispersal distance for cougars in Washington (unpublished data), and accounts for the fact that dispersal across real landscapes will have inherent resistance.

## Results

### Variable scales and transformations

For all cougars, males, and females, resistance to gene flow increased with increasing values of agriculture, building density, and road density (Table 2, Appendix 1). Resistance was lowest at moderate values of tree cover, grasslands, and rivers and streams. Resistance to gene flow decreased with increasing values of shrub and ridges. Responses to other variables differed by sex. All univariate models outperformed the isolation by distance hypothesis (Table 2). Females had larger scales of effect for elevation and canyons than all cougars, while males had a larger

**Table 2** Summary of best performing univariate resistance models by variable, scale, and transformation to resistance for male and female cougars (A; n=1902), females only, (B; n=902), and males only (C; n=902) in Washington, USA and south-central British Columbia, Canada, 2003–2018

Variable	Scale	Transformation	AICc	BIC	mR <sup>2</sup>	cR <sup>2</sup>
(A) Male and female						
<b>Elevation</b>	<b>500 m</b>	<b>Inverse ricker</b>	<b>− 4,239,938</b>	<b>− 4,239,875</b>	<b>0.1788</b>	<b>0.4436</b>
<b>Tree Cover</b>	<b>500 m</b>	<b>Inverse ricker</b>	<b>− 4,229,066</b>	<b>− 4,229,004</b>	<b>0.1223</b>	<b>0.3793</b>
Shrub	90 m	Negative monomolecular concave	− 4,228,210	− 4,228,148	0.1606	0.4303
Ruggedness	3000 m	Negative monomolecular concave	− 4,219,095	− 4,219,033	0.0826	0.3462
Rivers and streams	90 m	Inverse ricker	− 4,218,115	− 4,218,053	0.0870	0.3510
Grassland	3000 m	Inverse ricker	− 4,214,024	− 4,213,962	0.0987	0.3753
Agriculture	3000 m	Positive monomolecular concave	− 4,213,845	− 4,213,783	0.0895	0.3504
Building density	3000 m	Positive monomolecular convex	− 4,213,776	− 4,213,714	0.0940	0.3655
Canyons	500 m	Positive monomolecular concave	− 4,211,714	− 4,211,652	0.1060	0.3715
Road density	90 m	Positive monomolecular convex	− 4,211,433	− 4,211,371	0.0843	0.3522
Ridges	500 m	Negative linear	− 4,206,801	− 4,206,739	0.0785	0.3527
Euclidean distance	NA	NA	− 4,202,012	− 4,201,963	0.0633	0.3394
(B) Female						
<b>Tree Cover</b>	<b>500 m</b>	<b>Inverse ricker</b>	<b>− 959,643</b>	<b>− 959,589</b>	<b>0.1639</b>	<b>0.4137</b>
Elevation	3000 m	Negative monomolecular concave	− 958,209	− 958,154	0.1689	0.4257
<b>Shrub</b>	<b>90 m</b>	<b>Negative monomolecular concave</b>	<b>− 957,073</b>	<b>− 957,018</b>	<b>0.1720</b>	<b>0.4351</b>
Rivers and streams	90 m	Inverse ricker	− 955,093	− 955,039	0.1113	0.3635
<b>Agriculture</b>	<b>3000 m</b>	<b>Positive monomolecular concave</b>	<b>− 954,407</b>	<b>− 954,352</b>	<b>0.1186</b>	<b>0.3665</b>
Ruggedness	3000 m	Negative monomolecular concave	− 954,322	− 954,268	0.0997	0.3554
Road density	90 m	Positive monomolecular convex	− 951,613	− 951,558	0.0995	0.3640
Grassland	3000 m	Inverse ricker	− 951,438	− 951,383	0.1073	0.3821
<b>Building density</b>	<b>3000 m</b>	<b>Positive monomolecular convex</b>	<b>− 951,090</b>	<b>− 951,036</b>	<b>0.0987</b>	<b>0.3692</b>
Canyons	1500 m	Negative linear	− 950,841	− 950,787	0.0948	0.3642
Ridges	500 m	Negative linear	− 950,521	− 950,467	0.0948	0.3650
Euclidean distance	NA	NA	− 949,015	− 948,971	0.0742	0.3446
(C) Male						
<b>Elevation</b>	<b>500 m</b>	<b>Inverse ricker</b>	<b>− 941,164</b>	<b>− 941,559</b>	<b>0.1930</b>	<b>0.4416</b>
Shrub	1500 m	Negative monomolecular concave	− 936,532	− 936,477	0.1381	0.3962
Ruggedness	3000 m	Inverse ricker	− 935,213	− 935,158	0.0769	0.3315
Tree Cover	500 m	Inverse ricker	− 934,804	− 934,750	0.0941	0.3441
<b>Building density</b>	<b>3000 m</b>	<b>Positive monomolecular convex</b>	<b>− 934,650</b>	<b>− 934,596</b>	<b>0.0951</b>	<b>0.3501</b>
Grassland	3000 m	Inverse ricker	− 934,576	− 934,521	0.0960	0.3593
Canyons	500 m	Positive monomolecular convex	− 934,140	− 934,085	0.1110	0.3605
Rivers and streams	90 m	Inverse ricker	− 933,409	− 933,354	0.0704	0.3260
Road density	90 m	Positive monomolecular convex	− 933,268	− 933,213	0.0757	0.3293
Agriculture	500 m	Positive linear	− 932,546	− 932,491	0.0793	0.3333
Ridges	500 m	Negative linear	− 932,196	− 932,141	0.0685	0.3306
Euclidean distance	NA	NA	− 931,115	− 931,072	0.0545	0.3189

Model AICc and BIC values, and marginal and conditional R<sup>2</sup> values are reported. Variables in bold are variables that were in the best performing composite resistance surfaces. More information about composite resistance surface performance is provided in the text



scale of effect for shrub and a smaller scale of effect for agriculture.

For all cougars, the composite resistance surface with the lowest AICc value was comprised of elevation and tree cover (AICc = − 4,244,359, BIC = − 4,244,296; Table 2; Fig. 3a). No other composite resistance surfaces generated an AIC value that was 10 units from the top model. The top model had a marginal  $R^2$  of 0.1634. For females, the composite resistance surface with the lowest AICc value was comprised of tree cover, building density, agriculture, and shrub cover (AICc = − 962,602, BIC = − 962,547,  $mR^2$  = 0.1702; Table 2; Fig. 3b). For males, the composite resistance surface with the lowest AICc value was comprised of elevation and building density (AICc = − 941,283, BIC = − 941,229,  $mR^2$  = 0.1816; Table 2; Fig. 3c). To confirm the differences between males and females were not spurious results from our sample, we re-ran each male and female model with a random draw of half of the samples. The same top models for each sex were obtained (Appendix 3).

The top resistance surface for all cougars and females shows high resistance across the Columbia Basin. Other, subtle vegetative and topographic patterns in resistance can also be seen (Fig. 3a, b). The top resistance surface for males reflects high resistance in areas of high building density and low elevation (Fig. 3c). The resistant kernel connectivity surface for all cougars and females was similar, though the connectivity surface for females was more heterogeneous (Fig. 3d, e). For males, the connectivity surface had similar overall patterns to all cougars, but had higher genetic connectivity through the Columbia Basin, and lower on the Olympic Peninsula (Fig. 3f). The estimated local extent of breeding was 25 km for females and 100 km for males.

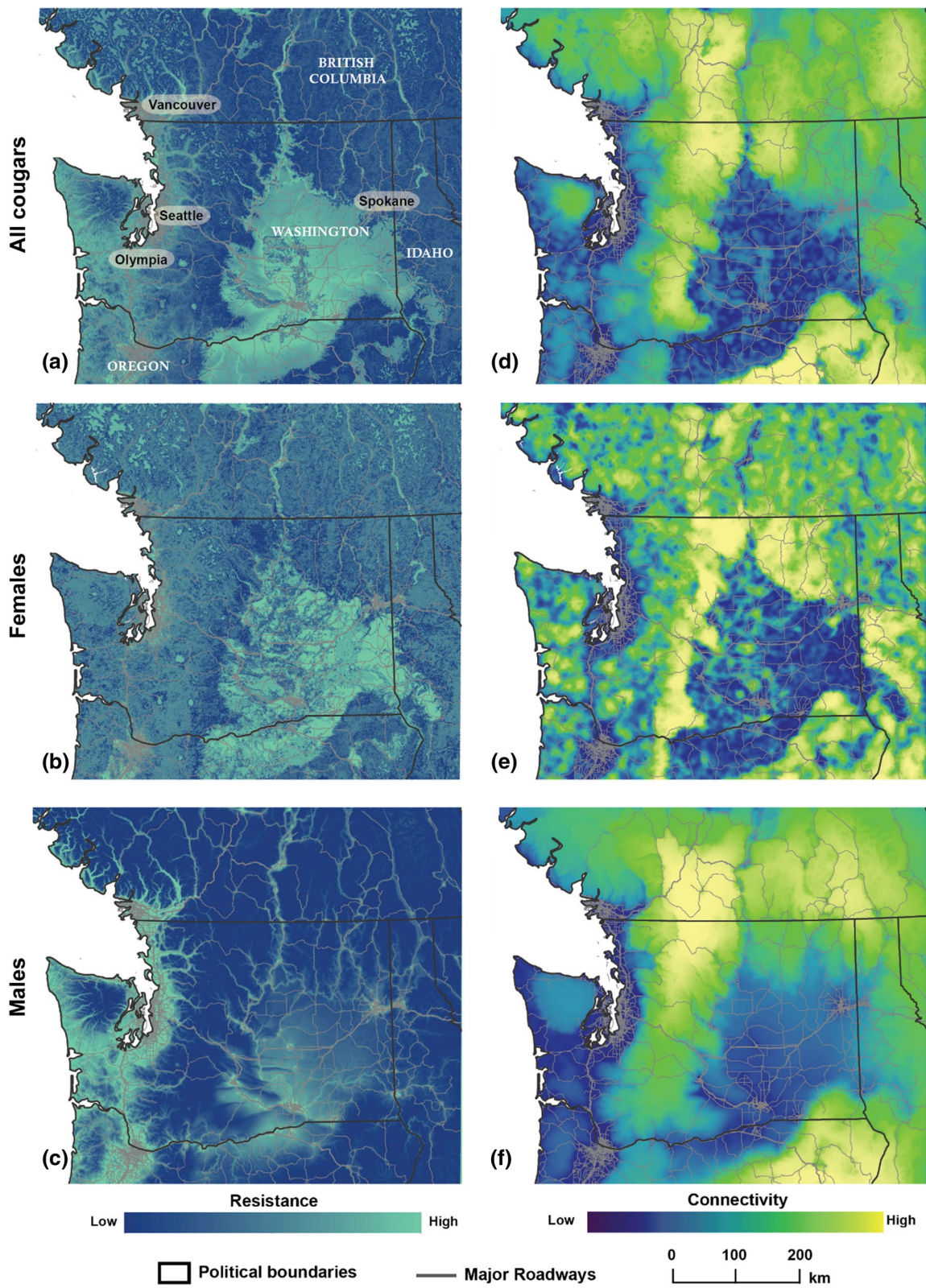
## Discussion

Our large dataset of 1902 cougar tissue samples allowed us to identify sex-specific landscape features affecting movement. In doing so, we found important differences between males and females. Females responded to more landscape features than males, and had more a more heterogeneous pattern to their resistance and connectivity surfaces, perhaps reflecting finer scaled movement decisions, or smaller breeding

extents. Across the whole study area, males generally had lower resistance and higher connectivity values, as well as larger continuous areas of high connectivity than females, especially in the Cascade Mountains and across the Columbia Basin. However, we also observed greater resistance to movement and a lack of connectivity for males in and around the Olympic Peninsula. This may indicate a more immediate management concern for the future of this population than previously reported (Warren et al. 2016).

Characteristics of both the male and female models were evident in the resistance and connectivity surfaces derived from our full sample of cougars, which contradicts our first prediction that males primarily drive genetic resistance for the whole population. The resistance surface and connectivity models for all cougars contained both the coarse features of the male model and the more heterogeneous features of the female model. The seemingly strong effect of females in the all-cougar model indicates local breeding and gene flow have important contributions to broader landscape scale inference. We did find females had, on average, a smaller breeding extent than males (25 km vs 100 km), which reflects generally smaller dispersal distances of females. These shorter movements indicate females may be interacting more strongly with local features on the landscape than males during successful dispersal events. There are two important implications of this finding for landscape genetic analysis with species exhibiting sex-specific dispersal behavior. First, if data from only one sex is available, inference about landscape feature effects on gene flow and connectivity may be limited. Second, if sample sizes are large enough, and there are sex-specific differences in breeding extents, analyzing data by sex can reveal important sex-specific patterns (Portanier et al. 2018).

Female cougars generally move shorter distances, and, thus, are more philopatric. For example, in the Black Hills of South Dakota, 40% of females were philopatric (Thompson and Jenks 2010). We also found females had smaller breeding extents and therefore do not typically disperse as far as males. Habitat selection during shorter dispersal events may follow similar selection patterns as home range resource use (Fattebert et al. 2015). However, selection during longer dispersal events may not follow similar selection patterns and individuals may be more tolerant of sub-par habitat during dispersal. Keeley et al. (2016)



**Fig. 3** Resistance and connectivity surfaces for all cougars (**a**, **d**), females (**b**, **e**), and males (**c**, **f**) in Washington, USA and surrounding areas, 2003–2018. Connectivity surfaces were derived using a cumulative resistant kernel connectivity model from source points distributed throughout the study area

proposed that the relationship between home range habitat suitability and resistance to movement during long distance dispersal events may be non-linear and recommended a negative exponential transformation that applied high resistance values to only the very lowest suitability values. Though not strongly supported, Zeller et al. (2018) found that some connectivity models for cougars in southern California performed slightly better with a negative exponential relationship from home range habitat suitability to resistance. Therefore, smaller dispersal movements, more typical of females, may more closely resemble home range use whereas longer dispersal distances more typical of males, may reflect more relaxed selection where avoidance is concentrated only in areas of very low suitability.

Our second prediction, that development would affect gene flow was partially supported. This result may be because of the inherent time lag between landscape change and when that change can be detected in genetic data (Landguth et al. 2010). Development was present in the male and female models, but not when both sexes were combined into a single analysis. However, in the all-cougar model, the combination of elevation and tree cover, both with an inverse ricker relationship to resistance, also resulted in high resistance values in heavily developed areas. This was likely due to very high resistances at low values of elevation and tree cover, which tended to correspond to developed areas. Although males and females had building density in their models, the resistance and connectivity surfaces show that males had a larger zone of effect for avoidance of highly developed areas. This aligns with other studies of cougars in more developed areas that have found higher use of developed areas by females, especially adult females accompanied by offspring, compared to males. For example, Benson et al. (2016) found females fed on mule deer closer to developed areas and further from riparian areas preferred by males, suggesting mortality risk for them or their offspring from encounters with males may be a factor. Alternatively, females with offspring may be more willing

to utilize areas of human development due to higher prey densities associated with rural and suburban areas (Holmes and Laundré 2006; Knopff et al. 2014; Wilmers et al. 2013). In western Washington, Kertson et al. (2013) found that though females had a lower percentage of development in their home ranges, they used developed areas more intensely than males. Furthermore, in the female models, tree cover seemed to partially mediate the negative effect of building density, whereas the final resistance model for males did not have tree cover.

Resistance surfaces ideally reflect movement, survival, and successful breeding. Using genetic data to estimate resistance can reflect all these factors. For example, the male surface reflects much higher resistance from the Cascades to the Olympics. Though cause and effect are difficult to infer, this may be a contributing factor to, or consequence of, the high level of inbreeding found for males on the Olympic Peninsula and surrounding areas compared to females (Wultsch et al. *in review*). Many carnivore species experience male biased dispersal, thus male gene flow is important for connecting isolated populations (Biek et al. 2006; Peck et al. 2017). The large dispersal events and associated mortality (Quigley and Hornocker 2010) that male cougars exhibit coupled with higher competition for mates (Logan and Sweanor 2010) and less opportunity for successful breeding than females may make them particularly vulnerable to landscape level resistance and reductions in genetic exchange. Although females are more philopatric, their smaller movements do not appear to influence inbreeding to the same extent as males (Biek et al. 2006).

Software programs like ‘ResistanceGA’ (Peterman 2018) and ‘radish’ (Pope and Peterman 2020) offer full optimization of resistance surfaces from genetic data. Due to our large sample size and study area extent, these options were not computationally feasible, and we opted for a pseudo-optimization approach. Though we could not explore the full parameter space, we tested seven relationships with resistance and multiple spatial scales and obtained ecologically meaningful results. Sampling design was another limitation of our study. Ideally, random, linear, or systematic sampling would be conducted (Oyler-McCance et al. 2013), but our samples were primarily based on hunter harvest and this opportunistic sampling over many overlapping years may



have biased our results. However, our sample size may have been large and distributed enough to counter these effects, and a random sample of these data resulted in similar results, indicating the robustness of the sampling.

### Conclusions/management implications

Most cougar populations are managed primarily using hunter harvest data, not genetics, to infer population status. Typically, unless harvest drops precipitously or hunter effort greatly increases, it is assumed that harvest numbers are indicative of the population and do not elicit management concern. Males are not generally considered as important for population persistence as females and considering harvest remains fairly steady, cougar abundance on the Olympic Peninsula would appear to be robust (WDFW, unpublished data). However, the high resistance levels we documented for male cougars suggest moderate concern for connectivity to other regions. Consequently, interpreting management needs from harvest or population numbers alone, may cause wildlife managers to be overconfident in the resilience of isolated populations.

Cougar home ranges can span hundreds of square miles, and clearly cross jurisdictional and political boundaries. Thus, it is likely that genetic management of cougars could be improved by establishing cross-jurisdictional collaborations to, for example, establish joint management zones and objectives. For instance, because our analyses suggest that cougars in the Blue Mountains are more isolated from other populations in Washington, genetic monitoring, and management of cougars here may be better served through partnerships with Oregon and Idaho wildlife agencies than with other populations in Washington.

Our findings also have immediate conservation value to managers. Our results highlight areas of lower connectivity along Interstate 5, but also highlight areas with relatively intact connectivity, providing movement options into and out of the Olympic Peninsula between Olympia, Washington and Portland, Oregon. With these maps, wildlife managers can begin the work of communication and collaboration with other land managers and government entities, including the Department of Transportation, with the intent of earmarking these areas for protection,

enhancement, and possibly even for wildlife crossing structures, thus aiding in wildlife dispersal and enhancing and perpetuating the exchange of genetic material. This information may also provide insight into recovery efforts for other species on the Olympic Peninsula such as translocated fisher (Lewis et al. 2022) or naturally recolonizing gray wolf populations (Maletzke et al. 2016). Understanding functional connectivity and how it relates to wildlife movement and maintenance of populations can provide important insights to wildlife managers.

**Acknowledgements** We wish to thank the biologists and officers from Washington Department of Fish and Wildlife (WDFW) for diligently collecting samples from all known cougar mortalities for use in this project. Also, thanks to Cathy Lacey and Brian Harris with British Columbia Ministry of Forests, Lands and Natural Resource Operations and compulsory inspectors for assistance collecting samples in BC. We thank the following hound handlers for volunteering their time and expertise on WDFW cougar research projects: R. Eich, B. Heath, K. Lester, D. Likens, T. MacArthur, K. Reber, S. Reynaud, C. Sanchez, B. Smith, C. Smith, M. Thorniley, B. Thorniley, and B. Trudell and M. White. We also thank Stephanie Simek and Brian Kertson for an early review of this manuscript. This research was supported in part by the USDA Forest Service, Rocky Mountain Research Station, Aldo Leopold Wilderness Research Institute. The findings and conclusions presented here are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy.

**Author contributions** K.Z. conceptualized and implemented the research approach, with consultation and input from C.W., L.W., R.B., and E.L. K.Z. wrote the initial manuscript with lots of contributions to the text by C.W., L.W., and R.B. All authors reviewed and edited the final manuscript drafts.

**Funding** This research was not supported by any external funds.

### Declarations

**Competing interest** The authors declare no competing interests.

### References

- Balkenhol N, Holbrook JD, Onorato D, Zager P, White C, Waits LP (2014) A multi-method approach for analyzing hierarchical genetic structures: a case study with cougars *Puma concolor*. *Ecography* 37:552–563
- Bartoń K (2019) MuMIn: multi-model inference. <https://R-Forge.R-project.org/projects/mumin/>

- Benson JF, Sikich JA, Riley SPD (2016) Individual and population level resource selection patterns of mountain lions preying on mule deer along an Urban-Wildland gradient. *PLoS ONE* 11:e0158006
- Biek R, Akamine N, Schwartz MK, Ruth TK, Murphy KM, Poss M (2006) Genetic consequences of sex-biased dispersal in a solitary carnivore: yellowstone cougars. *Biol Lett* 2:312–315
- Blaser N (2020) *rdist*: calculate pairwise distances
- British Columbia Government (2015) British Columbia Freshwater Atlas. British Columbia Geographic Warehouse. Downloaded from <https://catalogue.data.gov.bc.ca/datasets/freshwater-atlas-linear-boundaries>
- British Columbia (2019) Baseline thematic mapping present land use version 1 spatial layer. BC Geographic Warehouse. <https://catalogue.data.gov.bc.ca/dataset/baseline-thematic-mapping-present-land-use-version-1-spatial-layer>
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York
- Clarke RT, Rothery P, Raybould AF (2002) Confidence limits for regression relationships between distance matrices: Estimating gene flow with distance. *JABES* 7:361
- Compton BW, McGARIGAL K, Cushman SA, Gamble LR (2007) A resistant-kernel model of connectivity for amphibians that breed in vernal pools. *Conserv Biol* 21:788–799
- Crooks KR, Burdett CL, Theobald DM, King SRB, Marco MD, Rondinini C, Boitani L (2017) Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. *PNAS* 114:7635–7640
- Di Minin E, Slotow R, Hunter LTB, Montesino Pouzols F, Toivonen T, Verburg PH, Leader-Williams N, Petracca L, Moilanen A (2016) Global priorities for national carnivore conservation under land use change. *Sci Rep* 6:23814
- Ernest HB, Vickers TW, Morrison SA, Buchalski MR, Boyce WM (2014) Fractured genetic connectivity threatens a Southern California Puma (*Puma concolor*) population. *PLoS ONE* 9:e107985
- ESRI (2016) ArcGIS Desktop v.10x. Environmental Systems Research Institute, Redlands, California
- Fattebert J, Robinson HS, Balme G, Slotow R, Hunter L (2015) Structural habitat predicts functional dispersal habitat of a large carnivore: how leopards change spots. *Ecol Appl* 25:1911–1921
- Gilleland E (2013) Two-dimensional kernel smoothing: using the R Package Smoothie. NCAR Tech Note. <https://doi.org/10.5065/D61834G2>
- Gustafson KD, Gagne RB, Vickers TW, Riley SPD, Wilmers CC, Bleich VC, Pierce BM, Kenyon M, Drazenovich TL, Sikich JA, Boyce WM, Ernest HB (2019) Genetic source-sink dynamics among naturally structured and anthropogenically fragmented puma populations. *Conserv Genet* 20:215–227
- Hawley JE, Rego PW, Wydeven AP, Schwartz MK, Viner TC, Kays R, Pilgrim KL, Jenks JA (2016) Long-distance dispersal of a subadult male cougar from South Dakota to Connecticut documented with DNA evidence. *J Mammal* 97:1435–1440
- Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR, Kommareddy A, Egorov A, Chini L, Justice CO, Townshend JRG (2013) High-resolution global maps of 21st-century forest cover change: science 342(6160): 850–853. <http://www.sciencemag.org/content/342/6160/850.abstract>. Accessed from <https://www.glad.umd.edu/dataset/global-2010-tree-cover-30-m>
- Heller NE, Zavaleta ES (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biol Conserv* 142:14–32
- Holmes BR, Laundré JW (2006) Use of open, edge and forest areas by pumas *Puma concolor* in winter: are pumas foraging optimally? *Wbio* 12:201–209
- Jackson HB, Fahrig L (2015) Are ecologists conducting research at the optimal scale? *Glob Ecol Biogeogr* 24:52–63
- Jombart T (2008) adegenet: a R package for the multivariate analysis of genetic markers. *Bioinformatics* 24:1403–1405
- Jombart T, Ahmed I (2011) adegenet 1.3-1: new tools for the analysis of genome-wide SNP data. *Bioinformatics* 27:3070–3071
- Keeley ATH, Beier P, Gagnon JW (2016) Estimating landscape resistance from habitat suitability: effects of data source and nonlinearities. *Landsc Ecol* 31:2151–2162
- Kertson BN, Spencer RD, Marzluff JM, Hepinstall-Cyerman J, Grue CE (2011) Cougar space use and movements in the wildland–urban landscape of western Washington. *Ecol Appl* 21:2866–2881
- Kertson BN, Spencer RD, Grue CE (2013) Demographic influences on cougar residential use and interactions with people in western Washington. *J Mammal* 94:269–281
- Knopff AA, Knopff KH, Boyce MS, St. Clair CC (2014) Flexible habitat selection by cougars in response to anthropogenic development. *Biol Conserv* 178:136–145
- Landguth EL, Cushman SA, Schwartz MK, McKelvey KS, Murphy M, Luikart G (2010) Quantifying the lag time to detect barriers in landscape genetics. *Mol Ecol* 19:4179–4191
- Landguth EL, Hand BK, Glassy J, Cushman SA, Sawaya MA (2012) UNICOR: a species connectivity and corridor network simulator. *Ecography* 35:9–14
- Lewis JC, Jenkins KJ, Happe PJ, Manson DJ, Griffin PC (2022) Post-release survival of translocated fishers: implications for translocation success. *J Wildl Manag* 86:e22192
- Logan KA, Sweaner LL (2010) Cougar population dynamics. In: Hornocker MG, Negri S (eds) *Cougar ecology and conservation*. University of Chicago Press, Chicago, pp 105–117
- Maletzke BT, Wielgus RB, Pierce DJ, Martorello DA, Stinson DW (2016) A meta-population model to predict occurrence and recovery of wolves. *J Wildl Manag* 80:368–376
- Microsoft Building Footprint Data (2019) <https://github.com/microsoft/USBuildingFootprints> Microsoft
- McGarigal K, Wan HY, Zeller KA, Timm BC, Cushman SA (2016) Multi-scale habitat selection modeling: a review and outlook. *Landsc Ecol* 31:1161–1175
- McRae BH (2006) Isolation by resistance. *Evolution* 60:1551–1561



- Naidu A (2015) Where mountain lions traverse: insights from landscape genetics in Southwestern United States and Northwestern Mexico (Ph.D.). The University of Arizona, United States—Arizona
- Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods Ecol Evol* 4:133–142
- Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J (2022) *vegan*: Community Ecology Package. R package version 2.6-4. <https://CRAN.R-project.org/package=vegan>
- Open Street Map Contributors (2020) Planet dump. <https://download.geofabrik.de/north-america.html>
- Oyler-McCance SJ, Fedy BC, Landguth EL (2013) Sample design effects in landscape genetics. *Conserv Genet* 14:275–285
- Peck CP, van Manen FT, Costello CM, Haroldson MA, Landenburger LA, Roberts LL, Bjornlie DD, Mace RD (2017) Potential paths for male-mediated gene flow to and from an isolated grizzly bear population. *Ecosphere* 8:e01969
- Peterman WE (2018) *ResistanceGA*: an R package for the optimization of resistance surfaces using genetic algorithms. *Methods Ecol Evol* 9:1638–1647
- Peterman WE, Pope NS (2021) The use and misuse of regression models in landscape genetic analyses. *Mol Ecol* 30:37–47
- Peterman WE, Connette GM, Semlitsch RD, Eggert LS (2014) Ecological resistance surfaces predict fine-scale genetic differentiation in a terrestrial woodland salamander. *Mol Ecol* 23:2402–2413
- Pope NS, Peterman B (2020) Fast gradient-based optimization of resistance surfaces. <https://rdr.io/github/npope/radish/>
- Portanier E, Larroque J, Garel M, Marchand P, Maillard D, Bourgoin G, Devillard S (2018) Landscape genetics matches with behavioral ecology and brings new insight on the functional connectivity in Mediterranean mouflon. *Landsc Ecol* 33:1069–1085
- Quigley H, Hornocker M (2010) Cougar population dynamics. In: Hornocker MG, Negri S (eds) *Cougar ecology and conservation*. University of Chicago Press, Chicago, pp 59–75
- R Core Team (2021) R: a language and environment for statistical computing. Version 3.6.2. [WWW Document]. <https://cran.r-project.org/>. Accessed 12 June 19
- Row JR, Knick ST, Oyler-McCance SJ, Loughheed SC, Fedy BC (2017) Developing approaches for linear mixed modeling in landscape genetics through landscape-directed dispersal simulations. *Ecol Evol* 7:3751–3761
- Shirk AJ, Cushman SA (2011) sGD: software for estimating spatially explicit indices of genetic diversity. *Mol Ecol Resour* 11:922–934
- Shirk AJ, Cushman SA (2014) Spatially-explicit estimation of Wright's neighborhood size in continuous populations. *Front Ecol Evol* 2
- Shirk AJ, Landguth EL, Cushman SA (2017) A comparison of individual-based genetic distance metrics for landscape genetics. *Mol Ecol Resour* 17:1308–1317
- Shirk AJ, Landguth EL, Cushman SA (2018) A comparison of regression methods for model selection in individual-based landscape genetic analysis. *Mol Ecol Resour* 18:55–67
- Stoner DC, Rieth WR, Wolfe ML, Mecham MB, Neville A (2008) Long-distance dispersal of a female cougar in a basin and range landscape. *J Wildl Manag* 72:933–939
- Stoner DC, Wolfe ML, Choate DM (2006) Cougar exploitation levels in Utah: implications for demographic structure, population recovery, and metapopulation dynamics. *J Wildl Manag* 70:1588–1600
- Sweanor LL, Logan KA, Hornocker MG (2000) Cougar dispersal patterns, metapopulation dynamics, and conservation. *Conserv Biol* 14:798–808
- Thompson DJ, Jenks, JA (2010) Dispersal movements of subadult cougars from the Black Hills: the notions of range expansion and recolonization. *Ecosphere* 1:art8. <https://doi.org/10.1890/ES10-00028.1>
- Theobald DM, Stevens DL, White D, Urquhart NS, Olsen AR, Norman JB (2007) Using GIS to generate spatially balanced random survey designs for natural resource applications. *Environ Manag* 40:134–146
- U.S. Geological Survey (2016) Shuttle Radar Topography Mission (SRTM GL1) Global 30m Ellipsoidal. National Aeronautics and Space Administration. <https://dwtkns.com/srtm30m/>
- U.S. Geological Survey (2017) National hydrography dataset (NHD)—USGS national map downloadable data collection. USGS National Geospatial Technical Operations Center (NGTOC). <https://nhd.usgs.gov>. Accessed from <https://viewer.nationalmap.gov/>
- van Etten J (2017) R package gdistance: distances and routes on geographical grids. *J Stat Softw* 76:1–21
- Van Strien MJ, Keller D, Holderegger R (2012) A new analytical approach to landscape genetic modelling: least-cost transect analysis and linear mixed models. *Mol Ecol* 21:4010–4023
- Warren MJ, Wallin DO, Beausoleil RA, Warheit KI (2016) Forest cover mediates genetic connectivity of northwestern cougars. *Conserv Genet* 17:1011–1024
- Wilmers CC, Wang Y, Nickel B, Houghtaling P, Shakeri Y, Allen ML, Kermish-Wells J, Yovovich V, Williams T (2013) Scale dependent behavioral responses to human development by a large predator, the Puma. *PLoS ONE* 8:e60590
- Wright S (1946) Isolation by distance under diverse systems of mating. *Genetics* 31:39–59
- Wulsch C, Zeller KA, Welfelt LS, Beausoleil RA (in review) Genetic diversity, gene flow, and source sink dynamics of cougars in the Pacific Northwest. *Conserv Genet*
- Yang L, Jin S, Danielson P, Homer CG, Gass L, Bender SM, Case A, Costello C, Dewitz JA, Fry JA, Funk M, Granneman BJ, Liknes GC, Rigge MB, Xian G (2018) A new generation of the United States National Land Cover Database—requirements, research priorities, design, and implementation strategies. *ISPRS J Photogram Remote Sens* 146:108–123
- Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement: a review. *Landsc Ecol* 27:777–797

- Zeller KA, Vickers TW, Ernest HB, Boyce WM (2017) Multi-level, multi-scale resource selection functions and resistance surfaces for conservation planning: Pumas as a case study. *PLoS ONE* 12:e0179570
- Zeller KA, Jennings MK, Vickers TW, Ernest HB, Cushman SA, Boyce WM (2018) Are all data types and connectivity models created equal? Validating common connectivity approaches with dispersal data. *Divers Distrib* 24:868–879

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.